FEMORA

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INTRODUCTION

Fossil femora from Sterkfontein, South Africa have featured prominently in the history of human evolutionary thought and the recognition of *Australopithecus* as a bipedal hominin (Broom, 1938; Le Gros Clark, 1947; Broom and Robinson, 1949; Tobias, 1998). Femora discovered at the Sterkfontein Type Site by Robert Broom were described and functionally interpreted by Robinson (1972). Additional work by C. Owen Lovejoy (Lovejoy and Heiple, 1970; Heiple and Lovejoy, 1971; Lovejoy et al., 1973) helped frame the still-ongoing debate about hip function in *Australopithecus*. Since that time, many additional fossil femora have been recovered at Sterkfontein. While this is the first thorough description of these femora, others have commented on the state of preservation and morphology of these bones. Most notably, Harmon (2009a) detailed the preservation and morphology of the proximal femora and provided a thorough comparative analysis.

Likewise, DeGusta (2004) partially described the femora, though only in relation to the Bouri femur from the Middle Awash, Ethiopia. Here, we provide a detailed description of the Sterkfontein hominin femora, and additional comparative and functional interpretations of these fossils.

DESCRIPTIVE MORPHOLOGY

Felid femora

In a study of the MLD 46 femur, Reed et al., (1993) noted how similar fragmentary hominin femora can be to fossil felids and developed a methodology for distinguishing them. Most notably, the most inferior aspect of the femoral head is rounded off in hominin femora, but presents a hook-like anatomy in felids. Additionally, the fovea capitis is located more posteriorly and is not as centrally located in felid femoral heads compared with hominins. There are several proximal femora originally identified as hominin that are more likely felids (Reed et al., 1993; DeSilva, 2011). These include StW 30a, StW 30b, and StW 31 and are therefore not described in anatomical detail. The following specimens are all identified as hominin.

Sts 14: left proximal femur (Fig. 1; Table 1)

Preservation

Sts 14t is a poorly preserved left femoral neck and proximal shaft, preserving ~200 of the total length of the femur. The bone is crushed and consists of glued together fragments presumably held in the position of their discovery. The proximal most ~80 of the bone is badly cracked and held in place with glue but appears to have been recovered and preserved with the fragments in proper anatomical position. However, the more distal pieces are terribly distorted and result in the shaft bowing anteriorly in the sagittal plane and laterally in the coronal plane. Cortical bone along the shaft is crushed and flaking. The femoral head and posteromedial aspect of the neck are not preserved and have been reconstructed with plaster. Robinson (1972) reports that this reconstruction was made by R. Broom and based on part on a natural cast of the head preserved in breccia surrounding the fossil. Most of the femoral neck is present, but there is significant cracking and abrasion to the surface. The greater and lesser trochanters are sheared away. It is difficult to ascertain any shaft anatomy due to the extensive damage to the fossil.

[INSERT FIGURE 1 HERE]

Morphology

The femoral head is reconstructed with plaster to be ~28.8 superoinferiorly and ~29 anteroposteriorly. Robinson (1972) reports that the plaster head is 31—a measurement that can be replicated by measuring the head diagonally in the anteroinferior to posterosuperior direction. Based on the acetabulum of Sts 14, the head is likely to have been ~30.8 (Ruff, 2010). The neck is superoinferiorly tall: 22.6 superoinferiorly and approximately 14.2 anteroposteriorly, though the neck appears crushed and this is likely a minimum value. The femoral neck appears long, though it is not directly measureable given the absence of the head/neck junction. However, given that the head and neck reconstruction were based on a natural cast in the breccia, a morphological neck length of 27.9 can be estimated. Robinson (1972) estimates the neck-shaft angle to be 118 degrees. The trochanteric fossa is detectable just medial to the damaged surface for the greater trochanter. A portion of the intertrochanteric crest is palpable between the damaged trochanters. An obturator externus groove is not detectable. Robinson (1972) reports a faint linea aspera, spiral line, and gluteal ridge, but the specimen is tremendously damaged, fragmented, and distorted, so these features are unclear.

StW 25: right proximal femur (Fig. 2; Table 1)

Preservation

StW 25 is a fragmentary right femoral head and partial neck, primarily preserving the posterior part of the bone. Preserved overall is 39 mediolaterally and 30.7 superoinferiorly. The anterior aspect of the neck and part of the head is sheared away. The superior part of the femoral head is cracked and a 14.1 mediolateral fragment of the head is displaced superiorly by matrix, artificially expanding the head size. The crack extends medially and inferiorly under the fovea capitis. There is some erosion to the posterior surface of the head, including a 12.2 long, ~3 wide gash. The break in the femoral neck is obliquely oriented.

[INSERT FIGURE 2 HERE]

Morphology

The head is roughly 30.2 superoinferiorly. The anteroposterior head diameter is 30.4. Failure to account for the displaced fragment of bone on the superior head would result in a superoinferior head diameter closer to 32.0 mm. The fovea is large, deep and slightly offset posteriorly and inferiorly. It is 6.9 mediolaterally and 5.9 superoinferiorly. The neck height is 20.2 superoinferiorly. Superiorly, the ~13 mediolateral of preserved neck slopes gently from the head. Posteriorly, a lip of articular bone from the head extends onto the neck and grades smoothly into it. The cross-section of the neck reveals thick inferior and thin superior cortex.

StW 99/100: right proximal femur (Fig. 3; Table 1)

Preservation

StW 99/100 is a large right femur preserving the proximal 253 of the head, neck, and shaft. It consists of 3 pieces that have been reattached: 1.) a femoral head; 2.) 67 superoinferiorly of the neck and trochanteric region; and 3.) the remaining ~200 of the shaft. The first two pieces conjoin cleanly at the head/neck junction. The second and third pieces conjoin cleanly anteriorly, but there is a large gap separating them posteriorly. There is erosion around the perimeter of the head; articular surface of the head is only preserved anteromedially. The neck is quite well preserved. The greater trochanter is sheared away. The intertrochanteric crest is not preserved; there is a large gap between the lesser and greater trochanters where the larger two fragments of the fossil have been conjoined. Anteriorly, there is a small (~8) triangular shaped piece of bone missing where the larger two fragments of the fossil conjoin. The shaft is reasonably well-preserved, though there is some cortical flaking along the posterior aspect of the distal shaft. Anteriorly, there is a longitudinal crack running the length of the distal shaft piece.

[INSERT FIGURE 3 HERE]

Morphology

The minimum anteroposterior femoral head diameter is 35.5, though this is an underestimate given damage to the posterior surface of the head. Sphere-fitting techniques yield a femoral head diameter of roughly 39.1 mm (Ward et al., 2015), slightly larger than the estimated FHD of 38 (Ruff and Higgins, 2013) and slightly smaller than the 39.7 estimate (DeSilva et al., 2013). The neck is anteroposteriorly compressed and is 27.1 superoinferiorly and 19.1 anteroposteriorly. Anteriorly, the neck is smooth with no evidence for an intertrochanteric line. The posterior neck is smooth and laterally preserves some of the trochanteric fossa. Just medial to the fossa is a palpable obturator externus groove that continues inferomedially across the neck of the femur. The morphological neck length is an estimated 44. While there is no intertrochanteric line, a weak spiral line forms along the junction of the inferior femoral neck and medial shaft and merges with the lesser trochanter medially. A prominent pectineal line arches inferolaterally from the lesser trochanter and continues ~44 until it meets the gluteal line. Laterally, there is a prominent third trochanter/hypotrochanteric fossa complex which continues distally as a line that meets and then runs parallel with the pectineal line. This entire V-shaped region bounded by the pectineal line medially and the gluteal line laterally bulges from the posterior surface of the bone. Just inferior to the lesser trochanter, the subtrochanteric dimensions of the bone are 34.6 mediolaterally and 26.1 anteroposteriorly. Distally, the pectineal line and gluteal line merge into a prominent linea aspera. The shaft is mediolaterally expanded throughout and at the point of break in the distal shaft, the bone is 28 mediolaterally and 24.3 anteroposteriorly. Based on estimates of total length, the midshaft mediolateral width is between 28 and 28.4; the anteroposterior midshaft breadth is between 23.8 and 24.7. In lateral view, the shaft is slightly anteriorly bowed. The cortical thickness at the point of break in the shaft is 5.5 anteriorly, 6.6 posteriorly, 6.9 medially, and 7.1 laterally. Relative to the linea aspera, the head and neck of StW 99 are anteriorly angled.

StW 121: right femoral shaft (Fig. 4; Table 1)

Preservation

StW 121 is a distal right femur, preserving 204.1 from slightly above the midshaft to just superior to where the condyles would have been. The break near midshaft is obliquely angled so that more of the posterior surface than anterior surface is preserved, and shows little signs of wear on the broken surface. The posterolateral aspect of the surface near the break is slightly worn. The cortical bone of the shaft is generally well preserved, with some localized erosion. The distal end of the shaft is very worn, particularly on the anterior portion, where none of the patellar surface is preserved. The epicondyles and condyles have not been preserved. Because the anterior surface is worn this gives the distal end an angled appearance when viewed from the side.

[INSERT FIGURE 4 HERE]

Morphology

The shaft is cylindrical, with notable extension towards the posterior side for the linea aspera and posterolateral side. There is a strong linea aspera that begins below approximately midshaft and divides into distinct medial and lateral supracondylar lines. In anatomical view there is a strong lateral bow of the shaft. The minimum mediolateral width of the cortex mediolaterally is 8.9 at the proximal break. At approximately midshaft the mediolateral width is 25.2, anteroposterior width is 22.8. The mediolateral width of the distal end, which is notably worn on the lateral side is 42.5. The width of the shaft at the distal end at the last portion of the preserved surface is 20.1. The cortex measures 9.3 at the medial side and 9.6 at the lateral side.

StW 311: right proximal femur (Fig. 2; Table 1)

Preservation

StW 311 is a right femoral head and neck. The head is perfectly preserved. Only ~26 mediolateral of the neck is present, terminating in a jagged break. The posterior surface of the neck is well-preserved; the anterior is mostly sheared away exposing some trabecular bone. The inferomedial portion of the neck is still present. The neck is broken diagonally, roughly at the neck/shaft junction through the intertrochanteric crest. Preserved is 52 mediolaterally and 49 superoinferiorly.

Morphology

The femoral head diameter is 35.7 superoinferiorly and 35.6 anteroposteriorly. The fovea capitis is large, measuring 10.3 both superoinferiorly and mediolaterally. The head is large and globular—it is pinched off from the neck, except anteriorly, where it grades smoothly from the articular surface of the head onto the neck. The neck is 26.9 superoinferiorly and an estimated 19.3 anteroposteriorly. The preserved bone along the superior aspect of the neck slopes inferiorly from the head and angles superiorly, qualitatively suggesting a relatively short femoral neck. The posterior neck is smooth and terminates inferiorly with a small elevation that is likely the most proximal part of the lesser trochanter.

StW 361: proximal femur (Fig. 2; Table 1)

Preservation

StW 361 is a poorly preserved head and fragmentary neck of a likely right subadult femur. The anterior aspect of the femoral head is preserved, though there are patches of weathering anteriorly and superiorly; the posterior femoral head has been sheared away, exposing internal trabecular bone. A very small portion of the inferior neck is preserved. Overall, StW 361 is 35.4 mediolaterally.

Morphology

The superoinferior height of the femoral head is 29.1. Anteriorly, a prominent epiphyseal line is present indicating recent fusion of the capital femoral epiphysis and subadult status of this individual. Posteriorly, there is considerable damage, but the fovea can be identified and it is positioned inferior and posterior to the midpoint of the head.

StW 392: right proximal femur (Fig. 2; Table 1)

Preservation

StW 392 is a right partial femoral head and neck, preserving most of the head and posterior portion of the neck extending laterally 23.3. A small portion of cortex (6.5) has flaked from the lateral extent of the neck posteriorly, but otherwise the cortex is very well-preserved. The anterior aspect of the head and neck are sheared away, exposing trabecular networks. Total preserved dimensions are ~43 mediolaterally and ~37 superoinferiorly.

Morphology

The head is 31.5 superoinferiorly. It is offset from the neck inferiorly, but grades into the neck superoposteriorly. The fovea is offset posteriorly and somewhat inferiorly and is large, measuring 7.8 superoinferiorly and 10.1 mediolaterally. There is a faint epiphyseal line detectable posteriorly and inferiorly, suggesting that this femur belonged to a young adult. The neck height superoinferiorly is 19.2. Inferiorly, the neck is strongly convex, and pillar-like. There is a small piece of cortex preserved anteroinferiorly, allowing for a 13.7 minimum anteroposterior neck width, though this likely underestimates the true neck width. The oblique break through the neck reveals thick cortex inferiorly and thinner cortex superiorly.

StW 403: right proximal femur (Fig. 5; Table 1)

Preservation

StW 403 is a partial right femoral head and neck preserving 44.2 mediolaterally and 55.2 superoinferiorly. The entire inferior and much of the anterior aspect of the head is damaged, revealing trabecular bone and making any caliper-based femoral head diameter measurements suspect. Superiorly and posteriorly, the head is well preserved. The neck is well-preserved, but is sheared medial to the intertrochanteric crest. Anteriorly, there is a noticeable oval impression at the head-neck junction that may be carnivore damage (Harmon, 2009a)

[INSERT FIGURE 5 HERE]

Morphology

The preserved anteroposterior head diameter is 31.1, which is a minimum. Fitting a sphere to the head results in a more likely 32.7 (Ward et al., 2015). The fovea is slightly offset posteriorly and is 8.8 mediolaterally and 7.6 superoinferiorly. The superior rim of the fovea is elevated slightly above the articular surface of the femoral head. Posteriorly and somewhat superiorly, the head grades directly into the neck, without an obvious distinction between the two. The neck height is 24.4 and width 16.7, making the neck superoinferiorly tall. Posteriorly, there is a very small indentation along the neck that may be the medial extent of the obturator externus groove.

StW 448: right femoral shaft (Fig. 6; Table 1)

Preservation

StW 448 is roughly the distal third of a right femoral shaft, preserving 111.1. Proximally, where the shaft is broken, two spikes of shaft are located anteriorly and posteriorly. The surface of the bone has a series of cracks running superoinferiorly on the anterior and medial sides. There is a strong distinction between the cortical and trabecular bone on the distal break.

[INSERT FIGURE 6 HERE]

Morphology

There is a strong linea aspera that gives the shaft a distinctly elliptical shape and distally separates into slight lateral and medial supracondylar lines. The mediolateral width at the proximal end is 22.8; anteroposterior width is 22.3. The cortex at the proximal end is 7.7 laterally and 7.1 medially.

StW 479: right proximal femur (Fig. 5; Table 1)

Preservation

StW 479 is a partial right femoral head, neck, and part of the proximomedial shaft preserving 56 mediolaterally and 63 superoinferiorly. The anterior, superior and inferior aspect of the femoral head is eroded and the superior neck is eroded, exposing underlying trabecular bone. The fossil is sheared along the intertrochanteric crest, preserving only the most proximal tip of the lesser trochanter. The greater trochanter is not preserved. Cortical and trabecular bone are exposed at this break in the neck/shaft.

Morphology

The maximum anteroposterior width of the femoral head is 28.3, which is a minimum head diameter. Sphere-fitting techniques estimate a diameter of 32.7 (Ward et al., 2015). The fovea is offset posteriorly and inferiorly and is 8.8 mediolaterally and 5.3 superoinferiorly. There is a faint epiphyseal line along the head neck junction posteriorly, suggesting this femur belonged to a young adult. Posteriorly and superiorly, the head grades onto the neck without a clear distinction between the two. There is damage to the superior neck, though a small preserved portion of cortex allows for an estimated superoinferior height measurement of 23.5. The anteroposterior width is 17.4. Anteriorly, the neck is smooth with no evidence of an intertrochanteric line at the neck/shaft junction. Posteriorly, there is a slight but palpable depression marking the groove made by the tendon of the obturator externus muscle. A raised tubercle at the midline of the femoral neck is likely the quadrate tubercle. Using this landmark to delineate the likely path of the intertrochanteric crest, the morphological neck length of the femur is 32.6. A raised pillar of bone at the inferior neck shaft junction demarcates the proximal portion of the lesser trochanter.

StW 501: left proximal femur (Fig. 5; Table 1)

Preservation

StW 501 is a fragmentary and eroded left femoral head and neck preserving 53 mediolaterally and 48 superoinferiorly. The cortical shell of the head gone posteriorly, and eroded anteriorly and superiorly at the head/neck junction exposing underlying trabecular bone. There is pitting damage around the fovea capitis. Posteriorly, there is considerable damage along the neck, with only some cortex preserved superiorly. Anteriorly, a small (17 x 12) piece of cortical bone has flaked away exposing underlying trabecular bone and a crack runs mediolaterally from the head to this damaged cortical shell. The total neck length preserved is 32.6.

Morphology

The minimum preserved head diameter is 32.5; with an estimated actual size of ~33. The fovea appears to be more centrally located on this specimen compared with others and is approximately 7.5 mediolaterally and

7.9 superoinferiorly. Enough of the neck is preserved to estimate the superoinferior height of 23.4. The width is approximately 17.3, estimated because of damage to the anterior neck. The superior cortext of the neck is exposed and is notably thin.

StW 522: left proximal femur (Fig. 5; Table 1)

Preservation

StW 522 is a left proximal femur preserving the complete head, most of the neck and a small portion of the proximal shaft. The greater trochanter and lateral portion of the proximal shaft are not preserved at all; underlying trabecular bone is exposed. The lesser trochanter has been sheared away, exposing some underlying trabecular bone. Only the most proximomedial portion of the femoral shaft is preserved. There is abrasion caused either by carnivores or perhaps from mechanical preparation along the anterior portion of the head and neck. Total preserved amount of bone is 59.5 mediolaterally and 62.1 superoinferiorly.

Morphology

The femoral head is quite globular and strongly pinched off from the femoral neck except posteriorly and superiorly where they grade together. The articular surface of the femoral head, as viewed superiorly, is in a roughly neutral orientation. The femoral head is 30.9 anteroposteriorly and 30.4 superoinferiorly. The fovea is offset inferior and posterior and is 8.7 mediolaterally and 5.1 superoinferiorly. Superiorly, the notch of the femoral neck is preserved, including the far medial rim of the trochanteric fossa and the insertion region of the obturator externus muscle. The minimum neck height is 20.6 superoinferiorly; width is 15.2 anteroposteriorly. Posteriorly, there is a small portion of the intertrochanteric crest preserved, proximal and medial to which is a distinct obturator externus groove, which is 2.8 wide superoinferiorly. The mechanical neck length from the lateral rim of the femoral head to the intertrochanteric crest is ~31.

StW 527: proximal femur (Fig. 2; Table 1)

Preservation

StW 527 is a fragmentary and badly damaged femoral head, possibly from the left side. There is a matrix filled crack that separates the medial 2/3rds of the bone from the rest of the head. The two pieces remain physically connected, but they have shifted relative to one another. There is erosion at the junction between these two pieces as well, exposing some trabecular struts. Some cortex has flaked away from the rim of the fovea. Only a very small portion of the head/neck junction is present. Part of the neck is sheared exposing a network of trabecular bone. Overall, 38.6 mediolateral is preserved.

Morphology

The femoral head diameter, taken superoinferiorly on the larger preserved fragment is 32.2. The fovea is positioned inferior and posterior and is 9.2 mediolaterally and 7.5 superoinferiorly.

TM 1513: left distal femur (Fig. 7; Table 2)

Preservation

TM 1513 is 73.2 of the distal end of the left femur, preserved to about 50 above the patellar surface where the shaft is broken off at an angle to produce a sharp point of bone on the lateral side. The lateral aspect of the bone has been sheared away, removing the lateral epicondyle and a small portion of the lateral patellar surface. A small amount of abrasion is present on the top of the medial condyle. The surface cortex shows a fair amount of abrasion and pitting with sections of smooth cortical bone remaining. The popliteal surface is generally well preserved.

[INSERT FIGURE 7 HERE]

Morphology

The adductor tubercle is small but sharp and pronounced. Medially, just inferior to the medial epicondyle, there is a distinct groove running along the rim of the articular surface of the medial condyle. The condyles are asymmetrical with the medial side significantly larger than the lateral. The articular surfaces of both are well defined. The anteroposterior depth of the medial condyle is 45; the lateral is damaged anteriorly, but is likely about the same, estimated here to be 44. The maximum mediolateral width of the medial condyle is 22. The maximum width of the lateral condyle is 21.3. The intercondylar breadth is 13 and the height of the intercondylar notch taken from a line joining the most the inferior point of the medial and lateral condyles to the top of the notch is 12.2. The medial wall of the intercondylar notch indents slightly onto the medial condyle and marks the insertion for the posterior cruciate ligament. Along the posterior aspect of the lateral wall of the intercondylar notch is a distinct pit for the anterior cruciate ligament. The patellar surface depth is 2.6 in depth and 22.9 in height. There is some distinction between the cortical and trabecular bone at the break, with the cortex measuring 6.2 at its widest point.

Sts 34: right distal femur (Fig. 8; Table 2)

Preservation

Sts 34 is 69.3 of the distal end of a right femur, preserved to about 35.5 above the patellar surface where the shaft is cleanly broken off at an oblique angle with a greater amount of anterior than posterior surface preserved. Preservation is good, with the exception of some surface pitting, and a chip taken out of the surface superior to the patella surface. A large portion of the posterior surface of the medial condyle is missing and there is erosion to the posterior surface of the lateral condyle. The popliteal surface shows signs of abrasion and pitting.

[INSERT FIGURE 8 HERE]

Morphology

Posterolaterally, there is a small tubercle for plantaris superior to a larger insertion for the lateral head of gastrocnemius. Along the inferior rim of the lateral surface is a groove for the popliteus. Medially, there is a slight adductor tubercle. Both medial and lateral epicondyles are pronounced. The bicondylar breadth is 62.7. The condyles are asymmetrical with the medial side significantly larger than the lateral. There is a subtle groove on the medial side of the distal side separating the patellar from condylar surface. The articular surfaces are not well defined. The anteroposterior depth of the condyles cannot be determined due to breakage, though the lateral condyle from the eroded posterior surface to the rim of the lateral patellar lip is 45.1. Robinson (1972) estimates the medial condylar height to be 51.7. The maximum mediolateral width of the medial condyle is 21.9. The width of the lateral condyle is 19.3. The intercondylar breadth is 16.5. The height of the intercondylar notch is an estimated 16. A palpable indentation along the medial edge of the intercondylar notch delineates the insertion for the posterior cruciate ligament. The patellar surface depth is 5.5 and 24.2 in height measured from its most distal to most proximal point.

StW 129: left distal femur (Fig. 9; Table 2)

Preservation

StW 129 is a left lateral condyle and distal portion of the femoral shaft. It consists of two parts that have been neatly glued together; a fragment of the shaft and the remaining distal shaft and partial lateral condyle. The lateroposterior portion of the distal condyle is missing. The medial condyle is sheared away. There are three deep grooves running length wise on the popliteal surface, as well as at the break between the two portions. The anterior surface is well-preserved with a portion of the patellar surface.

[INSERT FIGURE 9 HERE]

Morphology

There is a distinct attachment for the lateral head of the gastrocnemius and a groove for the tendon of popliteus. The lateral epicondyle is distinct and well preserved. The anteroposterior depth of the lateral condyle is 47.3. The lateral condyle width is 20.8 mediolaterally, though there is some erosion making this a minimum. The superoinferior height of the articular surface of the condyle is 37.5 measured from the separation of the condylar and patellar articular surface demarcated by a shallow incurving of the lateral margin. In distal view, the lateral patellar lip rises strongly from the patellar surface. The cortex measures 3.5 at the lateral side. Overall dimension of the specimen is 59.1.

StW 318: right distal femur (Fig. 9; Table 2)

Preservation

StW 318 is a fragment of the lateral distal end of the right femur that includes the lateral condyle and epicondyle and more than half of the lateral portion of the patellar surface. All portions are fairly well preserved, with some wear on the lateral edge of the surface with exposed trabecular bone. The most proximal portion is represented by a shaft of bone. The lateral side including the epicondyle is well-preserved.

Morphology

Laterally, there are deep pits for the popliteus and lateral head of the gastrocnemius muscle. The anteroposterior height of the preserved lateral edge from the lateral patellar surface to the lateral condyle is 41. The maximum mediolateral width of the lateral condyle is 18.5, though the lateral margin in somewhat worn. The superoinferior height of the articular surface of the condyle is 24.7 measured from the separation of the condylar and patellar articular surface demarcated by a shallow incurving of the lateral margin—the total height of the lateral condyle including the lateral patellar lip is 41. In inferior view, the lateral patellar lip rises above the patellar surface. The cortex measures 1.5 at the lateral side. The overall length dimension of this specimen is 52.4.

COMPARATIVE MORPHOLOGY AND INTERPRETATION

Assignation to Members 4 or 5.

Most of the femora discussed in this paper were recovered from deposits clearly identified as Member 4. The proper geological context of two femora—StW 99/100 and StW 311—are discussed in more detail here. StW 99/100 is listed in the fossil catalogue in the hominin vault at the Evolutionary Studies Institute as deriving from Member 5, though we treat it here as coming from Member 4. StW 99/100 was recovered from grid W/45, depth 6'10"-7'10". This grid falls squarely within the boundary of Member 4 as determined by Kuman and Clarke (2000). Furthermore, Moggi-Cecchi et al. (2006) describe craniodental material from the same grid and similar depth—StW 116—and another fossil from similar depth and nearby grid, StW 104. StW 104 and 116 are from juveniles and are therefore not associated with StW 99/100 (an adult). However, these fossils are described as coming from Member 4, and are included in the *A. africanus* hypodigm (Moggi-Cecchi et al., 2006), suggesting that StW 99/100 was also recovered from Member 4.

Following Kuman and Clarke (2000), there is one fossil (StW 311) that derives from Member 5 East and could belong to early *Homo* or to *A. robustus*. While it remains possible that StW 311 is *Homo*, morphologically, it is quite similar to femora from Swartkrans that have been assigned to the robust australopiths. These include SK 82, SK 97, SK 14024, SKX 19, SKX 3121, and SKT1/LB-2. In a comparison of the femoral head to femoral neck height of hominin femora, StW 311 is most like three *A. robustus* femora, making this assignation reasonable (Fig. 10). Like other *A. robustus* femora (and unlike early eastern African *Homo* femora), StW 311 has an anteroposteriorly compressed (or superoinferiorly tall) femoral neck (Fig. 11).

Additionally, the ratio of the head diameter to neck breadth of StW 311 is outside the range of Sterkfontein Member 4 femora, and within the *A. robustus* sample (Fig. 12). For these reasons, we find it reasonable to tentatively assign StW 311 to *A. robustus*.

[INSERT FIGURES 10,11,12 HERE]

Mixed assemblage at Sterkfontein Member 4?

Clarke (1988, 2008, 2013) has posited the existence of a second, "pre-*Paranthropus*" species at Sterkfontein, and has resurrected *A. prometheus* with the discovery of StW 573 (Granger et al., 2015). Variation in proximal femoral anatomy has informed this discussion of anatomical variation in the Sterkfontein assemblage. Partridge et al. (2003) noted that the Jacovec cavern femur StW 598 possesses a small head and a long femoral neck, similar to the anatomy found in StW 99/100, and similar to the anatomy found in the Swartkrans *A. robustus* femora SK 82 and SK 97. However, StW 522 appears different in possessing a more globular femoral head and a short femoral neck.

Harmon (2009a) qualitatively assessed size and shape variation in the Sterkfontein femora and found that while size variation can easily be encompassed in a single variable species, shape variation is not as easily encompassed within a single taxon. With a larger sample that included all of the Sterkfontein femora, she found that StW 99 was an outlier and that it was most different from StW 522. It remains unclear how to interpret these findings, but several possibilities exist.

The femora at Sterkfontein may be sampling a single, highly-variable, quite dimorphic species. The work of Harmon (2009a) would appear to challenge this possibility. Alternatively, given the at least 600,000 years of sediment accumulation at Sterkfontein (Pickering and Kramers, 2010), the fossil assemblage may simply be picking up a single evolving lineage; high variation being the result of time-averaging. This effect may be exacerbated by the inclusion of a Member 5 East fossil (StW 311) into previous analyses. It could also be that, as Clarke (1998, 2013) has proposed, the Sterkfontein Member 4 assemblage consists of two species.

The apparent morphological differences between StW 99/100 and StW 522 would be consistent with this finding, though identifying which morph is best assigned to *A. africanus* and which morph to *A. prometheus* will require the comparison of each of these isolated elements to the extraordinarily complete template skeleton StW 573.

However, one final possibility that we currently support is that the eroded head of StW 99/100 has artificially inflated the apparent differences between StW 99/100 and StW 522. An eroded head and damaged intertrochanteric region makes it difficult to measure the morphological neck length—we place the value ~44 mm, slightly lower than the 46 mm in Partridge et al. (2003). Additionally, their estimate of 36 for the femoral head diameter is clearly too small (as is Harmon's (2009a) value of 34.6). Using a sphere-fitting technique, Ward et al. (2015) estimated the femoral head diameter of StW 99/100 to be 39.1. Using these values, the difference between StW 99/100 and StW 522 is not nearly as extreme. The long femoral neck may simply be because StW 99/100 is a larger individual than StW 522. When examined in the context of modern human femoral variation (Fig. 13), the neck length: head diameter ratio of StW 99/100 and StW 522 is easily encompassed within a single variable taxon. Thus, while there may very well be two taxa in Sterkfontein member 4, the proximal femora from Sterkfontein member 4 are morphologically more homogeneous than originally thought.

[INSERT FIGURE 13 HERE]

Functional anatomy

While Lovejoy's hypothesis that australopiths had a bipedal gait indistinguishable from that found in modern humans is often presented in the context of *A. afarensis* (e.g. Lovejoy, 1988), it originally was based on his observations of the Sterkfontein hip joint from Sts 14 and the distal femora Sts 34 and TM 1513 (Lovejoy and Heiple, 1970; Heiple and Lovejoy, 1971; Lovejoy et al., 1973). Compared with modern humans, Sts 14 possessed a long femoral neck and a small (reconstructed) femoral head. This combination of a long femoral neck and small femoral head, relative to humans today, is present in all of the Sterkfontein Member 4 femora (Fig. 13). Instead of regarding these anatomical differences as evidence for functionally different gait, Lovejoy et al. (1973) presented a biomechanical analysis in which the long femoral neck increased the mechanical advantage of the lesser gluteals (*Mm. gluteus medius* & *minimus*) during single-legged stance phase of bipedal walking. Because these muscles contracted with less force due to their insertion farther from the hip joint, the joint reaction force would be less in australopiths, explaining the relatively small femoral head. Furthermore, in the distal femur (Heiple and Lovejoy, 1971), *Australopithecus* possessed key anatomies for human-like bipedal gait, including a high bicondylar angle (14-15 degrees), an elevated lateral lip adaptive for patellar retention, and an elliptical lateral condyle adaptive for dissipating the high loads incurred on the knee during upright walking.

While most regard the Sterkfontein femoral material as good evidence for bipedalism in early hominins, and have for some time (Le Gros Clark, 1947; Broom and Robinson, 1949; Washburn and Patterson, 1951), there is evidence in the femur that the Sterkfontein hominins may have walked in a biomechanically different manner than humans today. Ruff and Higgins (2013) hypothesize that the subtle differences in cortical bone distribution in the femoral neck and the superoinferiorly reinforced femoral neck (Fig. 10) found in the Sterkfontein fossils is consistent with a small, but functionally significant, degree of lateral displacement of the body mass over the stance leg during gait. Subtle mediolateral sway of the body during gait would likely have been energetically less efficient, as would the, on average, shorter legs estimated for the Sterkfontein australopiths (Pontzer, 2012; Holliday, 2012, but see estimates of StW 99 leg length below).

Furthermore, attempts have been made to anatomically and functionally compare the Sterkfontein fossils to other hominin assemblages, particularly from Koobi Fora, Kenya, Swartkrans, and earlier australopiths from Hadar. Using StW 99, 311, 501, 522 and MLD 46 as representatives of *A. africanus* Harmon (2009b) found that these femora were generally similar to those from Swartkrans, Koobi Fora, and Hadar, but that *A. africanus* had quite low neck-shaft angles (especially StW 99 and MLD 46). McHenry and Berger (1998) noticed that while many of the isolated forelimb fossils from Sterkfontein were quite large, the femora were generally small (only StW 99 and 431were large enough to make the "medium" category). Green et al. (2007) quantified these observations using a resampling approach and agreed that the hindlimb joints (including the hip) of *A. africanus* was relatively smaller than that found in *A. afarensis*, signifying a potential difference in substrate use between the two australopith species. Tardieu (1981) suggested that the distal femora of *A. africanus* (TM 1513 and Sts 34) were quite human-like and similar to those from the Hadar 333 locality, but different from the A.L. 129 and A.L. 288 femora. McHenry (1986) disagreed and found the distal femora of *A. africanus* and *A. afarensis* to be quite similar. Lovejoy (2007) agrees and has regarded all australopith distal femora as possessing the key anatomies for human-like bipedal locomotion.

Sterkfontein and Hadar comparison

While we agree with others (e.g. McHenry, 1986) that the distal femora of *A. afarensis* and *A. africanus* are quite similar, we note here unrecognized and potentially functionally relevant differences in proximal femoral anatomy between fossils assigned to *A. afarensis* and those typically assigned to *A. africanus*. These are itemized below:

1. Compared with *A. afarensis*, the Sterkfontein Member 4 femora have slightly longer femoral necks relative to the size of the femoral head (Fig. 13; Table 3). Sample sizes remain low in both collections, but we find this an observation of interest, and of potential functional and evolutionary significance.

2. The proximal femora from Sterkfontein that are complete enough to preserve the anterior neck-shaft junction (n=2: StW 99/100 and StW 479) lack an intertrochanteric line. This rugosity, thought to signify extended hip posture and the tightening of the iliofemoral ligament, is present to varying degrees in all adult Hadar femora (n=4). A study on human femora found that those with relatively longer necks were more likely to lack an

intertrochanteric line, supporting a relationship between neck length and intertrochanteric line development (DeSilva et al., 2006), and consistent with the observation that *A. africanus* femora have longer necks than those assigned to *A. afarensis*. However, the functional link between these variables is currently unclear.

3. The neck shape index (anteroposterior breadth/superoinferior height) is slightly lower in *A. africanus* than in *A. afarensis* (Fig. 11)—in other words, the neck is more anteroposteriorly compressed (or superoinferiorly tall) in *A. africanus*. This difference is even more apparent when the anteroposterior breadth of the femoral neck is compared with the diameter of the femoral head (Fig. 12). In *A. africanus*, the head is considerably anteroposteriorly larger than the femoral neck, and there is no overlap whatsoever between the Sterkfontein and Hadar populations for this variable. The head of *A. africanus* extends more anteriorly than posteriorly, suggesting that *A. africanus* possessed slightly different hip mechanics (i.e. *A. africanus* may have been capable of more transverse plane rotation at the hip joint than was *A. afarensis*), or may reflect use of different substrates.

4. While the shape of the femoral midshaft is known from only one fossil (A.L. 288-1) and possesses a roughly circular shape, the two femoral midshafts from *A. africanus* (StW 99/100 and StW 121) are mediolaterally broad (Fig. 14), as found in some early *Homo* fossil and most *H. erectus* femora (Ruff, 1995).

In general, these findings—that the proximal femur of *A. afarensis* differs in subtle ways from *A. africanus*—are consistent with findings from the upper limb (McHenry and Berger, 1998; Green et al., 2007) and the foot (Harcourt-Smith and Aiello, 2004) that *A. afarensis* and *A. africanus* may have possessed slightly different walking mechanics (see also Harmon, 2009b). However, it remains noteworthy that there have been no differences found in the morphology of the distal femur in these two taxa (McHenry, 1998; Lovejoy, 2007; Squyres, 2016 but see Tardieu, 1981).

[INSERT FIGURE 14 HERE]

Internal anatomy

The internal structural anatomy of the Sterkfontein proximal femur (head and neck) has been studied using both conventional computed-tomography (CT) scanning and micro-CT scanning approaches. Chirchir et al. (2015) found that the femoral heads from Sterkfontein possess, on average, higher bone volume fraction (i.e. the highest density of trabecular bone per unit volume) than extant humans and apes, or other fossil hominins. The sampled fossils were StW 403 (36.6% bone volume/total volume, or BV/TV), StW 311 (47.5% BV/TV), and StW 527 (52.7% BV/TV). More recently, Ryan et al. (2018) discovered human-like orientation of the trabecular bone in femoral heads StW 99, 311, 392, 403, 479, and 501, indicating that *A. africanus* loaded their hips in a human-like way. Ruff and Higgins (2013) used conventional CT scans to quantify the distribution of cortical bone in the Sterkfontein hominin femoral necks, including: StW 99, 311, 403, 479, 501, and 522. They found human-like asymmetrical distribution of cortical bone at the neck/shaft junction. Only StW 99 possessed thickened superior bone outside the range typically found in modern humans. At the midneck, most of the specimens were in the human range (StW 99, 311, 403, 522). StW 479 was just outside the human range, while StW 501 was ape-like in possessing quite thick superior cortex. More recently, Claxton (2018) used higher resolution micro-CT techniques to quantify the cortical bone structure of the femoral necks and found Sterkfontein femora (StW 99, 311, 479, 501) to possess human-like ratios of superior to inferior cortex. However, the magnitude of superior cortex alone was thick and ape-like, inconsistent with predictions generated from human-like loading models of the hip joint (Claxton, 2018).

Size variation

Femoral head diameter is often used as a means for estimating body mass in fossil taxa. Fortunately, there are 11 proximal femoral head diameters that can be measured in the Sterkfontein collection. One of these, already discussed, is from Member 5 (StW 311). The other 10 are from Member 4, and may be from *A. africanus*. The smallest of these (StW 361) is from a juvenile and measures 29.1 mm. The largest (StW 99/100) is approximately 39.1 mm. Interestingly, the other eight are quite similar in size, ranging from 30.2-33.0 mm. It is difficult to know how to interpret this assemblage. It is of note that Pickering et al. (2004) has identified carnivore damage on many of these femora including definitive crenulation and tooth marks on StW 129 and 367; possible tooth marks on StW 25, 403, 479; and possible crenulation on StW 99, 121, 501, 522. It is possible that there was a sex-bias favoring smaller, presumably female, individuals in the accumulation of hominin remains at Sterkfontein (Lockwood, 1999).

Femoral length

Because a complete femur is not yet known from Sterkfontein Member 4 or 5, regression-based approaches have been used to estimate leg length from fragmentary fossils. However, these estimates have varied widely. Sts 14 is generally regarded as one of the shorter femora, with estimates ranging from between 276 mm (Steudel-Numbers and Tilkens, 2004) and 295 mm (McHenry, 1991) up to 310 mm (Broom et al., 1950). Lovejoy and Heiple (1970) estimated Sts 14 to have had a 280 mm leg length. Based on the femoral head diameters, StW 392 and StW 25 have yielded femoral length estimates of 311 mm and 320 mm respectively (McHenry, 1991). Vančata (1994) calculated femur lengths of 325 mm and 336 mm for the distal femora Sts 34 and TM 1513, though Steudel-Numbers and Tilkens (2004) estimate a lower 276 mm for Sts 34. Estimates vary the most for StW 99/100, ranging from 362 mm (Vančata, 1994) and 380 mm (McHenry, 1991) to as high as 433.5 mm (Holliday, 2012).

CONCLUSION

While a complete femur from Sterkfontein Member 4 or 5 remains elusive, enough fragmentary remains have been found to characterize the general femoral anatomy of these hominins. While some have postulated that the differences between StW 99/100 and StW 522 are evidence for taxonomic diversity, we regard these as large and small versions of the same general morphology. Multiple taxa may have been present at Sterkfontein; we just do not see evidence for it in the femora. However, while the distal femur of *A. africanus* is similar to that found in *A. afarensis*, the proximal femur is not. Sterkfontein Member 4 femora have relatively longer and more compressed femoral necks, and a large femoral head to femoral neck ratio. Whether these subtle morphological differences reflect differences in substrate use, reflect differences in locomotor kinematics, or result in functional equivalency, remains unclear.

FIGURE LEGENDS

FIGURE 1. Sts 14t in posterior (left) and anterior (right) view. Notice that the femoral head and part of the neck is reconstructed with plaster and there is severe damage to the femoral shaft. Scale bar in centimeters.

FIGURE 2. Fragmentary femoral heads of (from left to right): StW 25, StW 311, StW 361, StW 392, and StW 527. Fossils are positioned (from top to bottom) in anterior, posterior, superior, and medial views. As discussed in the text, StW 311 is from Member 5 and may be from *A. robustus*, whereas the other fossils all derive from Sterkfontein Member 4. Scale bar in centimeters.

FIGURE 3. StW 99/100 in anterior (bottom left), lateral (bottom right), and superior (top) views. Scale bar in centimeters.

FIGURE 4. StW 121 in (from left to right) anterior, posterior, and lateral views. Scale bar in centimeters.

FIGURE 5. Femoral heads and necks from Sterkfontein Member 4 (from left to right): StW 403, StW 479, StW 501, StW 522. Fossils are positioned (from top to bottom) in anterior, posterior, superior, and medial views. Scale bar in centimeters.

FIGURE 6. StW 448 in (from left to right) anterior, medial, and superior views. Notice in superior view the well-developed linea aspera. Scale bar in centimeters.

FIGURE 7. TM 1513 in (top row from left to right) anterior, posterior, and inferior views; (bottom row from left to right) lateral and medial views. Scale bar in centimeters.

FIGURE 8. Sts 34 in (top row from left to right) anterior, posterior, and inferior views; (bottom row from left to right) medial and lateral views. Scale bar in centimeters.

FIGURE 9. Distal femora StW 129 (top row) and StW 318 (bottom row). Both fossils are positioned in (from left to right) anterior, posterior, inferior, lateral, and medial views. Scale bar in centimeters.

FIGURE 10. Relationship between femoral head diameter (x-axis) and femoral neck height (y-axis) in humans and fossil hominins. The line drawn through the data is a RMA regression characterizing the human sample. Ruff and Higgins (2013) remarked on the relatively superoinferiorly tall femoral necks in the australopiths. Here, we agree that for a given head diameter, the Sterkfontein femora have relatively tall (superoinferiorly) necks, though some (StW 392 and StW 99/100) fall precisely on the modern human regression line. Note the position of fossil *Homo*, directly on the human trend line. Additionally, note the position of StW 311 (Sterkfontein Member 4) which is within a cluster of three *A. robustus* femora from Swartkrans, South Africa. Data from Table 1 and DeSilva et al., 2013; Ward et al., 2015.

FIGURE 11. There is considerable variation in femoral neck shape (neck breadth divided by neck height) in modern humans. However, in general, australopiths have been characterized as having a more anteroposteriorly compressed (or superoinferiorly tall) femoral neck relative to modern humans and fossil *Homo* (though see *H. naledi*). While there is some overlap, the Sterkfontein Member 4 femora and slightly more anteroposteriorly compressed than those from *A. afarensis*. Boxplots illustrate the median value (black bars), 25th to 75th percentiles (gray boxes), range of values (whiskers), and outliers (circles). Data from Table 1 and DeSilva et al., 2013; Ward et al., 2015.

FIGURE 12. Left: StW 522 (top) is compared with A.L. 288-1 (bottom) in superior view. The scale bar is 10 mm. Note that while the breadth of the femoral neck is quite similar in the two fossils, StW 522 has a much

larger femoral head. Note as well that the expansion of the femoral head is directed anteriorly (to the left in the image). To the right, the relative size of the femoral head to the neck breadth is quantified. Notice that *A. afarensis* is modern human-like in these proportions while the Sterkfontein Member 4 femora are quite different and possess a more anteroposteriorly compressed neck relative to the head size. We hypothesize that this morphology would result in greater transverse plane rotation at the hip joint in *A. africanus* compared with *A. afarensis*. Boxplots illustrate the median value (black bars), 25th to 75th percentiles (gray boxes), range of values (whiskers), and outliers (circles). Data from Table 1 and DeSilva et al., 2013; Ward et al., 2015.

FIGURE 13. Left: StW 99/100 is mirrored to reflect the right side and a sphere has been positioned to estimate the actual (39.1 mm) diameter of the femoral head based on a sphere-fitting technique applied to the preserved anterior surface (Ward et al., 2015). Below StW 99/100 is the much smaller femur StW 522. The scale bar is 10 mm. Visual inspection (as presented in Partridge et al., 2003) would suggest StW 99/100 has a relatively longer morphological neck length than StW 522. To the right is the range of neck length to femoral head diameter in modern humans (R^2=0.12; P<0.001). Notice that all of the Sterkfontein Member 4 femora (red stars) have similarly long necks given the size of the femoral head and present the same level of variation one might find in a modern human assemblage. The shortest neck belongs to Sts 14. Notably, both the head diameter and the neck length are approximations measured from plaster reconstructions based on impressions of these elements left in the fossil breccia. It is likely that these measurements—especially the neck length—are not entirely accurate. Note as well that the Sterkfontein femora generally have longer necks than those from Hadar (n=3; blue asterisks).

FIGURE 14. Femoral midshaft dimensions are plotted in this graph. Notice that in general *H. erectus* possesses a platymeric femoral midshaft (Ruff, 1995). Additionally, the femora from Sterkfontein Member 4 have a similarly anteroposteriorly compressed femoral midshaft. The three estimates for StW 99/100 are based on the

different positions of the midshaft using three different overall length estimates of the bone. The platymeric midshaft of *A. africanus* is in contrast to A.L. 288-1, which possesses an anteroposteriorly expanded midshaft.

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